

***Batrachospermum latericum* sp. nov. (Batrachospermales, Rhodophyta) from Tasmania, Australia, with New Observations on *B. atrum* and a Discussion of Their Relationships**

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Abstract

Batrachospermum latericum sp. nov. occurs in humic streams in the Southwest National Park in Tasmania and is thus far collected from New Harbour to the Old River catchment. Like *B. diatyches* Entwisle, also a Tasmanian endemic, the thallus of the new species has brick-like rhizoidal filament cells and a large apical cell. The primary fascicles, however, are more like those of *B. puiggarianum* Grunow from South America and Africa. New character states, including the sporadic occurrence of spermatangia on involucre bracts and 'shortly indeterminate' gonimoblast filaments, are reported for the widespread *B. atrum* (Hudson) Harvey. There is no support for the recognition in Australia or New Zealand of the recently described *B. androinvolucrum* Sheath *et al.*, characterized by the production of spermatangia exclusively on involucre filaments. In an exemplar cladistic analysis based on morphological characters, taxa included currently in the section *Setacea* formed a monophyletic clade and within this, the two Australian endemics were sister taxa. Brick-like rhizoidal filament cells, a large thallus apical cell and shortly indeterminate gonimoblast filaments are derived character states within Batrachospermales.

Introduction

The setaceous species of *Batrachospermum* (section *Virescentia* p.p.; = section *Setacea* *sensu* Sheath *et al.* 1993a) from Australia and New Zealand were revised six years ago (Entwisle 1992). Since that revision, a new species has been discovered in Tasmania, additional collections of *B. atrum* (Hudson) Harvey have revealed more character variation within that taxon, and a revision of North American representatives of this group has been published by Sheath *et al.* (1993a). The description of the Tasmanian species and an analysis of new data are presented here in advance of a complete account of the order Batrachospermales for the *Algae of Australia* series (see also Entwisle and Foard 1997). A cladistic analysis based on morphological characters is used to assess the monophyly of the section *Setacea* (considered to be part of *Virescentia* by Necchi and Entwisle 1990), and to study the distribution of brick-like rhizoidal filament cells, large thallus apical cells and shortly indeterminate gonimoblast filaments in the Batrachospermales.

Methods

Preparation of Material

Specimens were preserved initially in 5% commercial formalin or, less suitably for microscopic examination, in 70% ethanol. After preparing dried specimens and permanent microscope mounts, the remaining material was transferred to 70% ethanol with 5% glycerol. Microscope preparations were stained with 1% aniline blue (with 4% HCl) and mounted in 10% Karo corn syrup (and 0.25% phenol), with 40% Karo corn syrup (and 0.25% phenol) added to the side of the coverslip during drying

Cladistics

The data matrix was constructed using Dada (Nixon 1995) and run in Nona (Goloboff 1993) with the 'multi*' option. Random addition sequences were run 35 times holding 35 trees at each run. The shortest trees were examined using Clados (Nixon 1994).

Data were taken from the series of revisions published by R.G. Sheath, M.L. Vis, K.M. Cole and co-authors (Kaczmarczyk *et al.* 1992; Sheath *et al.* 1993b, 1994b; Vis and Sheath 1992; see Entwisle, 1998, for *Batrachospermum* references) because their species concepts match those used in the previously published molecular analysis of this group (Vis *et al.* 1998). Representative material in MEL was also examined.

Descriptions of Species

1. *Batrachospermum latericum* Entwisle sp. nov.

a *B. puiggariano* Grunow cellulis filamentarum rhizoidalium lateriformibus (8–15 μm diametro), cellula apicali thalli largiore (11–15 μm diametro), carposporangii largioribus (20–26 μm longo, 16–18 μm diametro), et trichogynio obovoideo ad fusiformem differt; a *B. atro* (Hudson) Harvey proprietatibus omnibus praecedentibus et verticillis reductis maxime (plerumque bicellularibus) ad axem centralem adhaerentem differt; a *B. diatychite* Entwisle fasciculis primariis brevioribus, ad septum constrictum et cellula apicali thalli per fasciculos protrusum differt. Figs 1, 2A

Type: Tasmania, Southwest National Park, Old River, first major riffle above Bathurst Harbour, Entwisle 2507, 4.iii.1996 (holotype MEL; isotype HO).

Thallus firm, monopodial, 1–5 cm long, olive-green; apices acute, apical cell 6–12 μm long, 11–15 μm in diameter, protruding through primary fascicles.

Fascicle whorls conical, very small and often barely rising above rhizoidal filaments, 99–180 μm in diameter, separated; internodes 120–170 μm in long. *Axis* colourless, axial cells 40–80 μm in diameter, rhizoidal filament cells brick-like, 7–12 μm long, 8–15 μm in diameter, narrow secondary rhizoidal filaments (cells 10–16 μm long, c. 6 μm in diameter) sometimes present between primary rhizoidal filaments in older thalli; first fascicle initials produced 1–4 cells proximal to apex (2-celled fascicles present 4–6 cells proximal to apex). *Secondary fascicles* either a single cell cut-off from primary rhizoidal filament or a short filament arising from secondary rhizoidal filament. *Primary fascicles* 2 or 3 per pericentral cell, of 2(–4) cell storeys, branching absent or once-dichotomous; proximal cell obovoid (to globose), c. 8 μm long, c. 8 μm in diameter; distal cells globose (to hemispherical or dome-shaped), 6–10 μm long, c. 6 μm in diameter; hairs common in young part of thallus, up to 12 μm long. *Monosporangia* absent.

Monoecious (but individuals usually either predominantly male or female). *Spermatangia* borne on primary and secondary fascicles, clustered, globose, c. 8 μm in diameter. *Carpogonia* borne on (or in place of) primary fascicles, 1–2 cells from periaxial cell, subtending cells 4–5 μm long, 6–8 μm in diameter, scarcely modified; involucrel filaments arising from all subtending cells, not extending beyond carpogonium, 1–2 cells long; carpogonium more or less straight, c. 22–24 μm long, base symmetrical or slightly oblique, c. 6 μm in diameter, trichogyne sessile, obovoid to fusiform, 7–10 μm in diameter at broadest part. *Carposporophytes* 1 per whorl, exerted from whorl, semi-globose, compact, c. 160 μm in diameter (c. 6 times whorl radius), centred on node; gonimoblast filaments 2–3 cells long; post-fertilisation cells of carpogonial branch obscure; carposporangia obovoid or globose, 20–26 μm long, 16–18 μm in diameter.

Chantransia rarely observed, sparsely branched; cells cylindrical, 38–56 μm long, 8–10 μm in diameter.

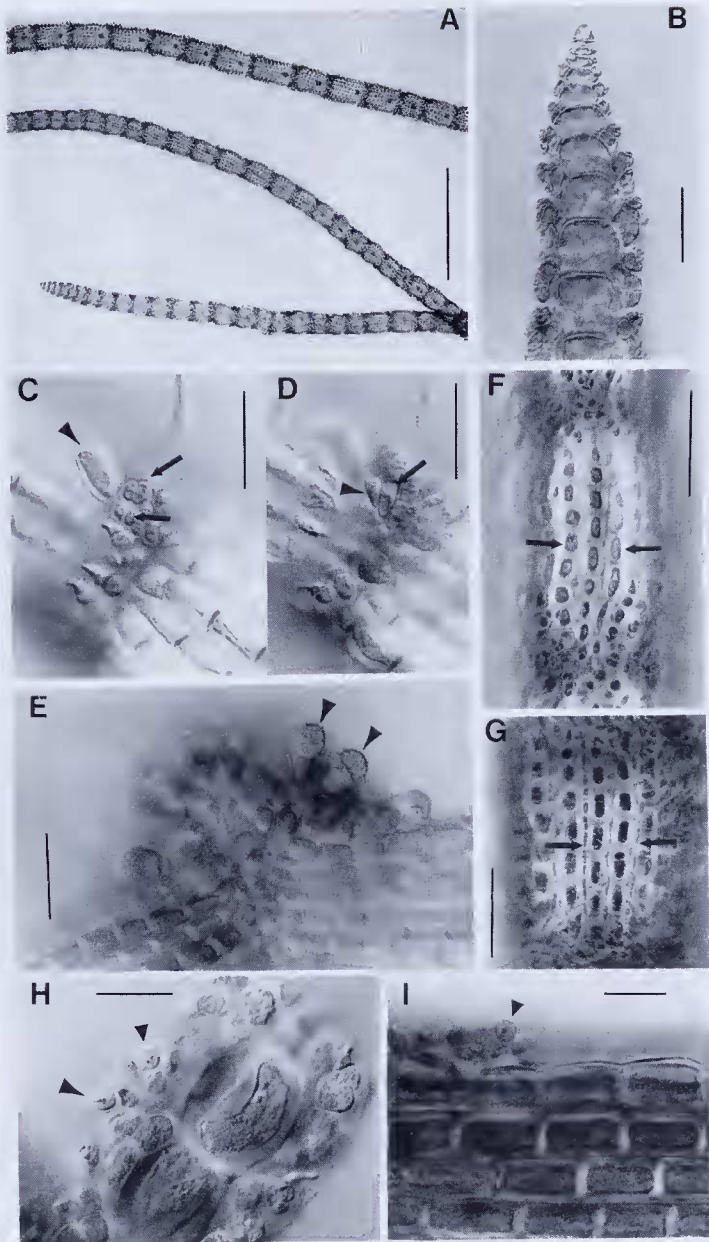


Fig. 1. *Batrachospermum latericum* Entwisle & Foard sp. nov. **A** thallus showing reduced whorls and regular rhizoidal filament cells (Entwisle 2534). Scale: 1400 μ m. **B** apex showing fascicle initiation and structure (Entwisle 2534). Scale: 150 μ m. **C** nodal region of thallus showing trichogyne (arrowhead), involucre bracts (arrows) and reduced fascicles (Entwisle 2547). Scale: 150 μ m. **D** same as C but focusing on the base of the carpogonium (arrowhead) and carpogonial branch (arrow). Scale: 150 μ m. **E** gonimoblast with carposporangia (arrowheads) (Entwisle 2547). Scale: 150 μ m. **F** brick-like rhizoidal filament cells (arrows) (Entwisle 2534). Scale: 200 μ m. **G** brick-like rhizoidal filament cells and narrow secondary rhizoidal filaments (arrows) in older part of thallus (Entwisle 2534). Scale: 200 μ m. **H** spermatangia (arrowheads) on primary fascicles in young part of thallus (Entwisle 2507). Scale: 100 μ m. **I** spermatangia (arrowhead) on secondary fascicle (older part than H) arising from brick-like rhizoidal cells (Entwisle 2507). Scale: 50 μ m.

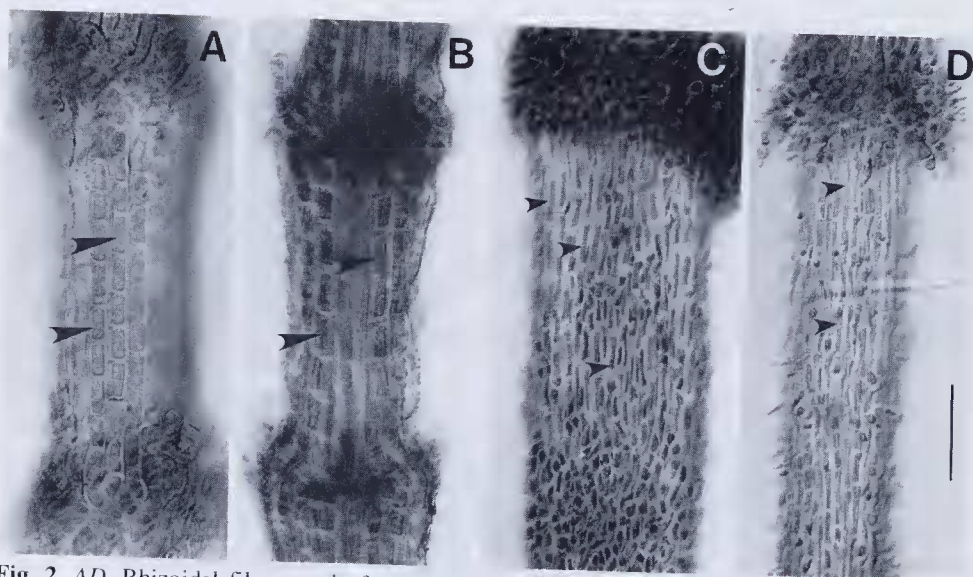


Fig. 2. AD, Rhizoidal filaments in four *Batrachospermum* species (Section *Virescentia*). Scale 200 μm . *Batrachospermum latericum* (A) and *B. diatyches* (B) with comparatively broad, brick-like rhizoidal filaments (large arrowheads); *B. puiggarianum* (C) and *B. atrum* (D) with cylindrical rhizoidal filaments.

Diagnostic Features

Batrachospermum latericum differs from *B. puiggarianum* Grunow (Fig. 2C) by having brick-like rhizoidal filament cells which are 815 μm in diameter (cf. 4 μm in diameter), a large thallus apical cell (11–15 μm cf. c. 7 μm in diameter), larger carposporangia (20–26 μm long and 16–18 μm in diameter cf. 8–13 μm long and 6–11 μm in diameter) and an obovoid to fusiform trichogyne (cf. club-shaped to ellipsoid). It differs from *B. atrum* (Figs 2D, 3) in all of the above features and by having extremely reduced whorls (usually 2 cells cf. 3–6 cells long) closely adherent to the central axis. *Batrachospermum diatyches* (Fig. 2B) has similar apical cells and rhizoidal filaments to *B. latericum* but the fascicles of that species consist of 4–6 cells in a tapering filament without constrictions at the cross-walls, and the thallus apical cell is overtopped by fascicles.

Distribution and Habitat

Batrachospermum latericum is restricted to streams in the far south-west corner of Tasmania, sometimes occurring with *B. atrum*. The streams are all humic-rich (tea-coloured) and flow through Button Grass (*Gymnoschoenus sphaerocephalus*) heath and cool temperate rainforest.

Etymology

From the Latin *latericum* (= brickwork), referring to the regular arrangement of rhizoidal filament cells diagnostic of this species and fellow Tasmanian endemic *B. diatyches*.

Other Specimens Examined

Tasmania: Southwest National Park: waterfall in New Creek, flowing off E side of SW Cape Ra., New Harbour, Entwisle 2547, 7.iii.1996 (MEL, HO); creek c. 1 km NNW of Smoke Signal Hill, first creek crossed on South Cape Track from New Harbour to Melaleuca, Entwisle 2556, 6.iii.1996 (MEL, HO); waterfall in creek flowing NNW from Harrys Bluff, c. 1 km SE of confluence with Old River, Entwisle 2543, 6.iii.1996 (MEL, HO); same creek as previous but in small water drop near confluence with Old River, Entwisle 2534, 6.iii.1996 (MEL, HO).

Notes

Although the reduced whorls are superficially similar to *B. puiggarianum*, the thallus apical cell and rhizoidal filaments of *B. latericum* are similar to those of *B. diatyches*. In addition, *B. latericum* and *B. diatyches* are restricted to cool temperate habitats in Tasmania, while *B. puiggarianum* is known only from tropical to subtropical South America and Africa (Necchi 1990a, Sheath *et al.* 1993a). The cladogram presented below indicates a possible relationship between these taxa.

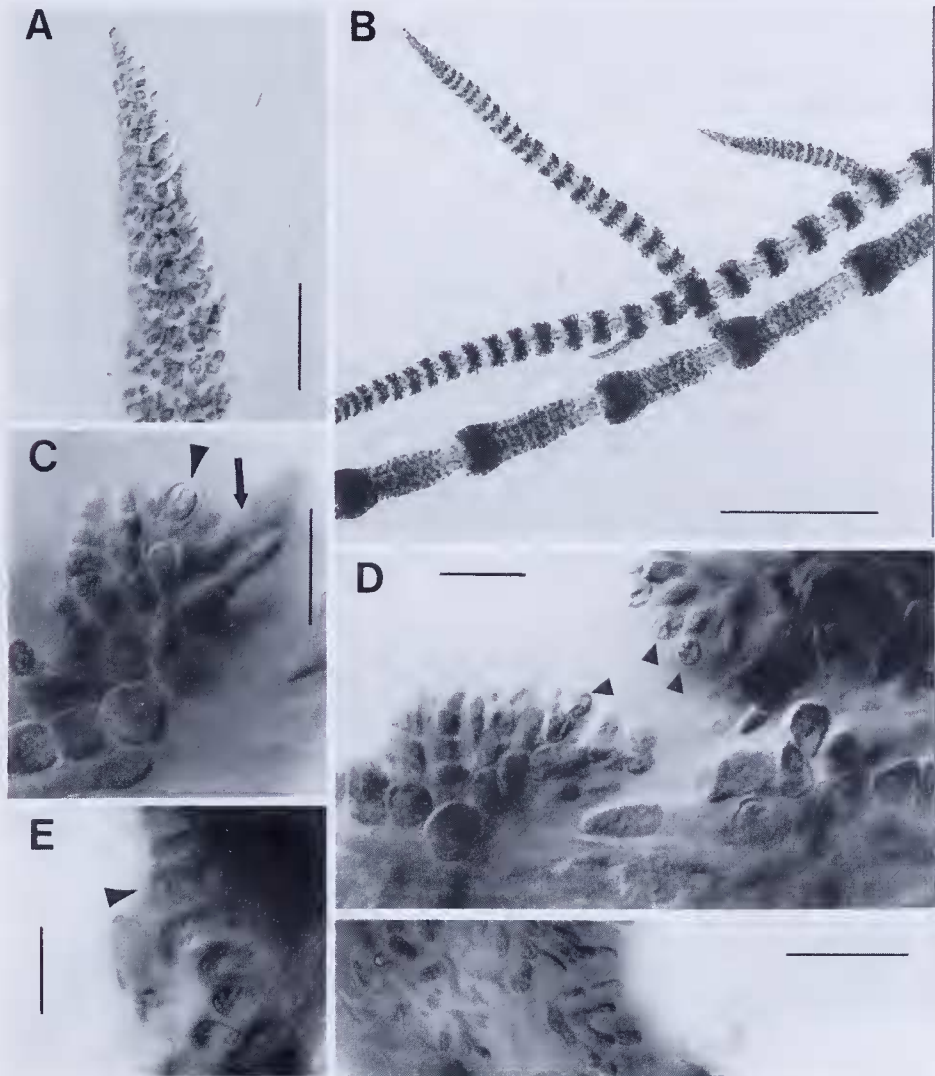


Fig. 3. *Batrachospermum atrum*. **A** apex of thallus showing fascicle initiation and hairs (Entwistle 2520). Scale: 150 μ m. **B** thallus showing comparatively well developed whorls (Entwistle 2516). Scale: 1000 μ m. **C** carpogonial branch showing spermatangia (arrowhead) on involucral bracts and carpogonium (arrow) (Entwistle 2233). Scale: 50 μ m. **D** spermatangia on primary fascicles (arrowheads) (Entwistle 2233). Scale: 50 μ m. **E** indeterminate gonimoblast filaments (arrows) extending beyond determinate portion of gonimoblast (arrowhead) (Entwistle 39). Scale: 50 μ m. **F** indeterminate gonimoblast filaments extending along internodal region of thallus (arrows) (V. Stout [SI]). Scale: 100 μ m.

2. *Batrachospermum atrum* (Hudson) Harvey

Additions to the description in Entwisle (1992, p. 430): internodes 160–1100 μm long; rhizoidal filaments 3–9(–21) μm in diameter, sometimes inflated; secondary fascicles sometimes absent; spermatangia borne on involucrel filaments as well as on primary or secondary fascicles and sometimes on specialised fascicles, occasionally extremely profuse; carpogonial branches borne on (or in place of) secondary fascicles (as well as primary fascicles), carpogonia straight or curved, sometimes only 11–14 μm or up to 60 μm long, trichogyne to 11 μm wide in broadest part; carposporophyte up to 230 μm in diameter, occasionally borne internodally; gonimoblast filaments sometimes shortly indeterminate (i.e. they extend a short distance along the axis away from the primary carposporophyte mass); centre of carposporophyte sometimes distant from axis in older thalli.

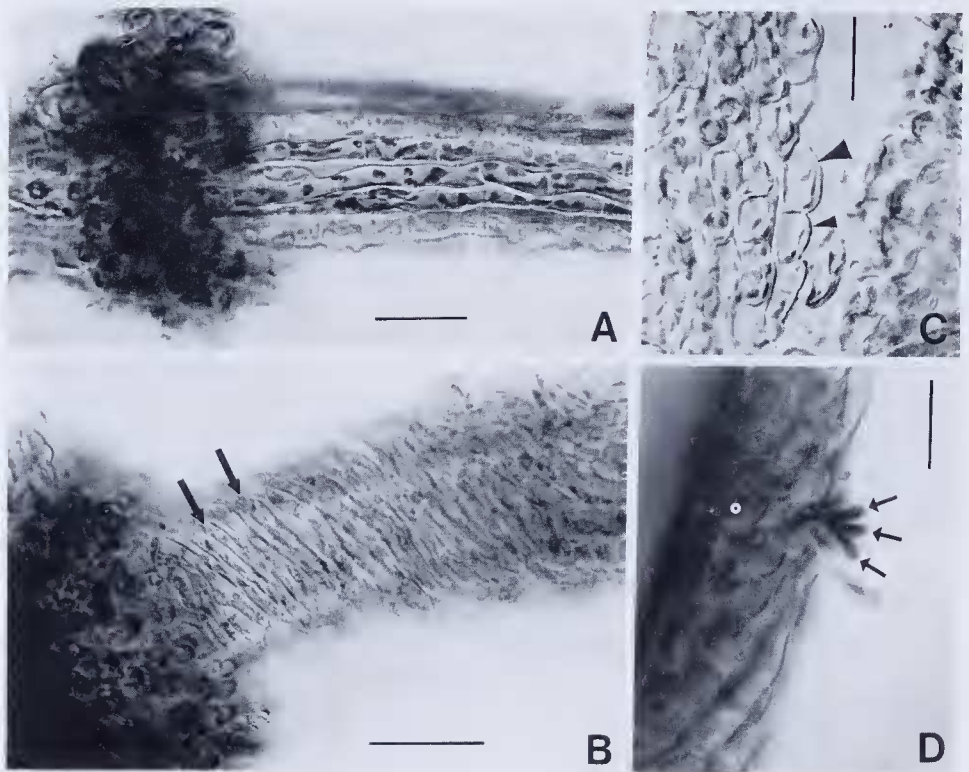


Fig. 4. *Batrachospermum atrum* (Lake Mountain variant) (Entwisle 2445). **A** younger portion of thallus with cylindrical rhizoidal filaments. Scale: 200 μm . **B** spiralling rhizoidal filaments (arrows). Scale: 200 μm . **C** squashed portion of thallus showing inflated rhizoidal cells (arrowheads). Scale: 100 μm . **D** internodal carpogonial branch (arrowhead) with involucral bracts terminated by elongate cells (arrows). Scale: 100 μm .

Selected Specimens Examined¹

Western Australia: Beedelup Falls, c. 16 km W of Pemberton, *Entwisle 2403*, 6.i.1994 (MEL, PERTH); Frankland River, Hazelvale, *Entwisle 2397*, 6.i.1994 (MEL, PERTH); South Dandalup River, Torrens Road, c. 14 km NEE of Pinjarra, *Entwisle 2381*, 5.i.1994 (MEL, PERTH). **Queensland:** Running Creek, Kilcoy-Beerwah Road crossing, 2 km NE of Stanmore, *Entwisle 2232*, 6.ix.1993 (MEL, BRI). **Tasmania:** creek into Bathurst Harbour, W side of channel S of Forest Lagoon, *Entwisle 2516 and 2520*, 4.iii.1996 (MEL, HO); creek into New Harbour, W of New Creek, *Entwisle 2553*, 7.iii.1996 (MEL, HO); tributary of Great Forester River, Scottsdale-Derby Road, c. 8 km E of Scottsdale, *Entwisle 2625*, 12.iv.1996 (MEL, HO). **Victoria:** Delegate River (West Branch), Gunmark Road, 4.5 km from Gap Road, *Entwisle 2133*, P.Y. Ladiges, G. Nelson and R. Raleigh, 8.i.1992; (MEL); creek flowing through Echo Flat, near Helicopter Flat, Lake Mountain, *Entwisle 2445*, 30.xii.1994 (MEL).

Notes

Inflated Rhizoidal Filament Cells: Young portions of some thalli from Barren Grounds (New South Wales; *Entwisle 1566*) and Beedelup Falls (Western Australia; *Entwisle 2403*) have rhizoidal filament cells somewhat inflated but becoming cylindrical with age. This feature is unlikely to be homologous with the inflated rhizoidal cells in the mature thalli of some species in the section *Batrachospermum* (Vis *et al.* 1995) and does not appear to have any taxonomic utility in *B. atrum* (i.e. it does not correlate with any other features and there is some variability within and between individuals).

Spermatangial Distribution: Spermatangia were commonly borne on involucre bracts (Fig. 3C) in specimens referable to all three groups delineated by Entwisle (1992). In contrast to the North American specimens studied by Sheath *et al.* (1993a), spermatangia were not restricted to involucre filaments (diagnostic of *B. androinvolucrum*) or only vegetative fascicles (*B. atrum*): see Fig. 3C and D. This less discriminating distribution of spermatangia is similar to that reported for species such as *B. confusum* and *B. speruatoinvolucrum* (section *Batrachospermum*), and *B. globosporum* (section *Contorta*) (Sheath *et al.* 1993a, Vis *et al.* 1995, Vis and Sheath 1996). In the absence of collaborating characters, and because this feature seems to cross all intuitive taxonomic boundaries (i.e. the three groups of Entwisle 1992), the Australian populations are retained within *B. atrum*.

Some collections from Tasmania (*Entwisle 2516, 2520, 2625*) had very distinctive 'clipped poodle'-like whorls as have been noted before in some Group B (*sensu* Entwisle 1992) specimens of *B. atrum*. Such specimens produced an abundance of spermatangia on primary and secondary fascicles. However, profuse spermatangia can occur in collections with other whorl morphologies (e.g. *Entwisle 2397*).

Carpogonium Size: One collection from Western Australia (*Entwisle 2403*) had very small carpogonia (not more than 14 μm long). However, the material was overmature and carpogonia were difficult to locate and score. Until further material is collected this aberration is assumed to be yet further variation in *B. atrum*.

Carposporophyte Size: The carposporophytes scored were sometimes up to 250 μm in diameter (and larger when apparently two or more became intertwined; *Entwisle 1921*). This size range, from 100–230 μm in diameter (i.e. broadest dimension of semi-globose mass) is similar to that reported for *B. atrum* by Sheath *et al.* (1993a); although *B. atrum* has often larger carposporophytes than *B. androinvolucrum* Sheath *et al.*, the range of the former includes entirely that of the latter.

¹From 36 localities additional to those reported in Entwisle (1992). Collection details of specimens referred to in text but not documented here can be found in Entwisle (1992).

Indeterminate Gonimoblast Filaments: In a number of specimens examined (e.g. Entwisle 39, 2233, 2381, 2553, 2445), some gonimoblast filaments extended along the axis beyond the main carposporophyte mass (Fig. 3E, F). These filaments appear to be technically indeterminate (producing short carposporangial filaments laterally and never terminated by a carposporangia) but of limited growth. They appear to be homologous with the gonimoblast filaments observed in *B. terawhitiui* but of more limited growth. Similar filaments are produced in some populations of *B. turfosum*: homology of these states is tested in the cladistic analysis.

Carposporophyte Position in Whorl: In specimens from Dargans Creek (New South Wales; Entwisle 1921, Entwisle 1925) the gonimoblast begins as sessile on the axis but becomes stalked and centred away from the axis in older thalli. Again, there does not seem to be any taxonomic utility in this feature.

Lake Mountain variant: A specimen from Lake Mountain National Park (Victoria; Entwisle 2445) had inflated rhizoidal filament cells up to 21 μm in diameter (Fig. 4C; but cf. Fig. 4A), rhizoidal filaments spiralled (rope-like) around the axial filament in some mature parts (Fig. 4B). Secondary fascicles were absent in some parts (where rhizoidal filaments were inflated and spiralling) and common in other parts, sometimes bearing carpogonial branches. Carpogonia varied considerably in size yielding measurements outside previous ranges for *B. atrium*: 25–54(–60) μm long and trichogyne 4–11 μm in diameter at broadest part. The involucre bracts were terminated by elongate cells (to 15 μm ; 4D), which may have been spermatia (although spermatia of a size and shape typical of *B. atrium* were observed on fascicles). This population warrants further study, but none of these features in isolation or in combination warrant the establishment of a new taxon at this stage.

Cladistic Analysis

Characters

All characters used to define taxa in the Batrachospermales were assessed for the cladistic analysis. Some were autapomorphies and were excluded as uninformative. Others were too poorly documented or inconsistently applied: e.g. trichogyne shape was too variable within taxa as well as being difficult to circumscribe as a character.

The following characters are used in the analysis.

0. *Thallus* multiaxial (0) or uniaxial (1). Only *Thorea* is multiaxial but autapomorphies in outgroups are informative.
1. *Thallus apical cell diameter*: c. 4–8 μm (0), 10–15 μm (1). The broad apical cells of *B. diatyches* and *B. latericium* tend to be hemispherical as well as relatively broad, but further documentation in other taxa is required before shape can be used as a phylogenetic character. The degree to which the apical cell protrudes from the whorls of fascicles also warrants further study. The scoring of apical cell diameter in *Lemanea fluviatilis* is based on equivocal observations from dried herbarium material of this species at MEL, as well as generalisations on the family from the illustrations of Atkinson (1890) and Bourrelly (1985) and personal observations by M. Vis-Chiasson on *Paralemanea*. However, Sheath (1984) includes photographs of *L. fucina* with apical cells 4–8 μm , and the scoring of this character in *L. fluviatilis* should be verified (particularly given its reversal in the two shortest trees).
2. *Fascicle adherence*: partly or not at all (0), complete (1). *Tuomeya* and *Lemanea* have completely adhering outer cortical layers, unlike any other taxa considered here.

3. *Rhizoidal filament cell shape*: elongate (0), brick-like (1). See taxonomic section above for definition of brick-like rhizoidal filament cells. Rhizoidal filaments are absent in *Leuanea fluviatilis* and not applicable in *Thorea*.
4. *Fascicle cell storeys*: 5 or more (0), 1–6 (1). To be scored as 0, at least some fascicles on each individual must have 7 or more cell storeys. The ‘fascicles’ of *Lemanea fluviatilis*, if traced from the axis to the outer cortex, are more than 5 cells long.
5. *Fascicle cell shape*: audouinelloid (0), not audouinelloid (1). See Necchi (1990b) for definition of audouinelloid filaments.
6. *Monosporangia* present (0) or absent (1). The presence of monosporangia in *Thorea* requires confirmation (Necchi and Zucchi 1997) and *T. violacea* has been split into two entities, one with monosporangia, the other without.
7. *Spermatangia on involucreal filaments* (1) or not (0). Although the presence of spermatangia on involucreal filaments distinguishes *B. androinvolucrum* from *B. atrum*, as mentioned earlier some populations of *B. atrum* from Australia have spermatangia on involucreal filaments as well as elsewhere in whorls. *Batrachospermum atrum* is divided into four taxa to represent variation in this character and character 16. The absence of spermatangia on vegetative filaments is an autapomorphy for *B. androinvolucrum* and is not included in this analysis.
8. *Carpogonial branches* arising mostly from intercalary fascicle cells (0) or exclusively from periaxial cells or proximal cell of fascicles (1). The differentiation of carpogonial branches is variable within the group studied, and is difficult to categorize (see e.g. Entwisle and Foard 1997). However the origin of what is generally accepted as ‘the carpogonial branch’ seems to fall into the two categories defined here (sometimes it is difficult to distinguish between an origin from the periaxial cell and the proximal fascicle cell, so a strict scoring of periaxial cell only seemed too impractical).
9. *Carpogonial branches* straight (0) or curved to spiralled (1). *Lemanea* generally seems to have somewhat curved carpogonial branches (see Atkinson 1890) but carpogonial branches in this genus are difficult to observe and seldom described.
10. *Carpogonial branch length*: never more than 5 cells long (0), usually 5 or more cells (1). The unbranched filament subtending the carpogonium is considered to be the carpogonial branch in all taxa.
11. *Carpogonial base* more or less symmetrical (0) or strongly asymmetrical (1). The carpogonial bases in *Sirodotia* and *Tuomeya* are clearly symmetrical in relation to the trichogyne pedicel. All other taxa have a symmetrical or slightly oblique carpogonial base in relation to the trichogyne pedicel.
12. *Trichogyne longevity*: not persisting after fertilisation (0), persisting after fertilisation (0).
13. *Trichogyne shape*: linear (0) or swollen (1). More precise characterisation of trichogyne shape was not possible due to variation reported within currently circumscribed species.
14. *Trichogyne attachment*: sessile (0) or pedicellate (1). See Sheath *et al.* (1986) for definition of ‘pedicellate’ vs ‘sessile’. The trichogynes of *Sirodotia suecica* and *Tuomeya americana* are somewhat intermediate in terms of pedicel definition but they have been scored here as pedicellate. When the trichogyne is linear (character 13 = 0), this character is inapplicable.
15. *Carposporophyte* with determinate filaments bearing carposporangia clustered around the carpogonium (1) or not (0). If no carposporophytes are produced (as in *B. turfosum* 1), this character is inapplicable.
16. *Indeterminate gonimoblast filaments*: present (0) or absent (1). Inapplicability as for character 15. The carposporophytes of *Thorea* (Necchi pers. comm.), *Sirodotia* and *Nothocladus* consist of long indeterminate filaments giving rise

laterally to branched determinate filaments bearing clusters of carposporangia. 'Shortly indeterminate' filaments, extending a relatively short distance from a mass of determinate gonimoblast filaments, are found in some species of *Batrachospermum*. There is some debate about the validity of this feature (e.g. Sheath *et al.* 1994a) but it has been confirmed in at least some populations of *B. atrum* (this study) and *B. turfosum* (Kumano *et al.* 1970, as *B. vagum*). For this reason these two taxa have been divided to account for this variation (see also note under character 7 regarding *B. atrum*). The inclusion of 'short' and 'long' indeterminate gonimoblast filaments as a separate character state resulted in an unacceptably large number of trees due to the predominance of the inapplicable character state in the matrix (i.e. for all taxa lacking indeterminate gonimoblast filaments). This character requires further study.

17. *Carposporophytes per whorl*: 1 or 2 per whorl (0), usually more than 2 (1). If the thallus is multi-axial (character 0 = 0) or carposporophytes are not produced (as in *B. turfosum* 1), this character is inapplicable.
18. *Carposporophytes 'centred'*: variously in whorl (0), on axis (1), on outside cortical layer (2). See Entwisle & Foard (1997) for definition of centred. If determinate gonimoblast filaments are absent (character 15 = 0) or carposporophytes are not produced (as in *B. turfosum* 1), this character is inapplicable. Treated as non-additive in analysis.
19. *Carposporophytes in whorl*: fully embedded (0), protruding (1). Inapplicability as for character 18.

Taxa

The data matrix (Appendix 1) included all taxa currently included in the section *Setacea/B. atrum* complex, as well as species chosen to represent the major clades of the consensus tree based on combined 18S and rbcL data in Vis *et al.* (1998). *Psilosiphon scoparium* has no known sexual reproduction and has been excluded from the study (all but 4 characters would be scored 'not applicable'). *Tlorea* was chosen as the outgroup based on the results of Vis *et al.* (1998). When *Rhododraparnaldia* was included in our matrix it was placed as sister to *B. diatryches* in all shortest trees. However as we were unable to include *Audouinella arcuata* and *Palmaria palmata* (part of the clade including *Rhododraparnaldia* in the molecular trees) due to lack of sufficient comparable data, this relationship was probably an artefact of overall similarity.

Results and Discussion

70 shortest trees of branch length 56 with a CI of 37 and an RI of 41 were found. The Nelson consensus tree is shown in Fig. 5. In all shortest trees the section *Setacea* (*B. androinvolucrum*, *B. atrum*, *B. diatryches*, *B. latericium* and *B. puiggarianum*) is monophyletic, and the two Tasmanian endemics *B. diatryches* and *B. latericium* are sister taxa. The proposal by Necchi and Entwisle (1992) to include the setaceous species in section *Virescentia* (represented here by *B. helmintiosum*) is not supported. Instead there is weak support for a close relationship between the sections *Turfosa* and *Setacea*.

The consensus tree is poorly resolved overall and shows little congruence with that produced from the combined molecular data set by Vis *et al.* (1998, fig. 3). For example, the relationship between *Sirodotia* and *Lemanea* is unresolved in our consensus tree, but strongly bootstrap-supported as a monophyletic clade with the combined molecular data. Unfortunately, the paraphyly of *Batrachospermum s. str.* and *Batrachospermaceae* as clearly demonstrated in Vis *et al.* (in press) is neither

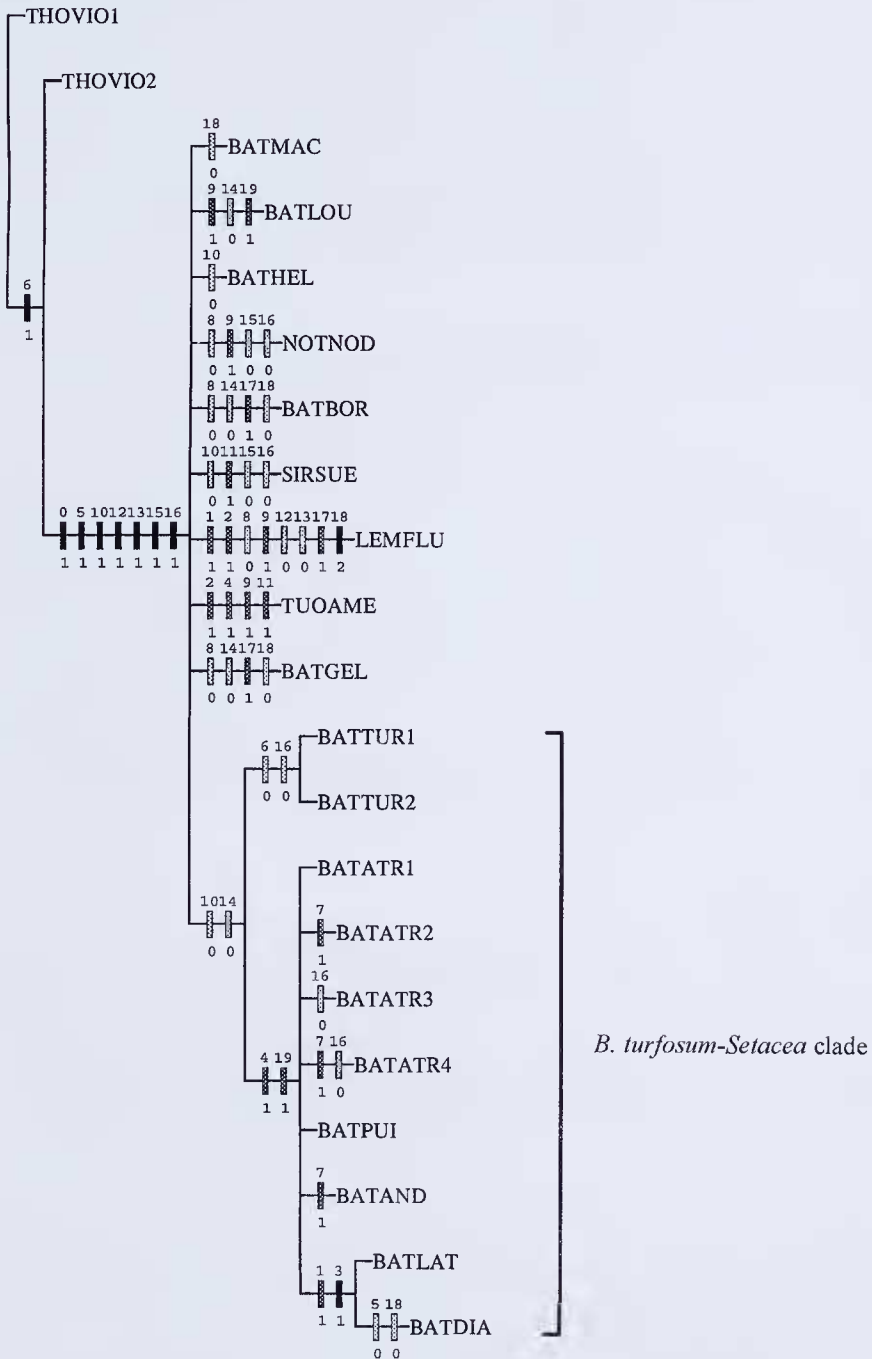


Fig. 5. Strict consensus tree from the 70 shortest trees using Nona (with multi* option) on data in appendix 1 with *Thorea violacea* 1' as outgroup. L = 56, CI = 37, RI = 41. The taxa are designated by the first three letters of the genus followed by the first three letters of the species.

supported nor opposed in our tree. While the tree presented here supports the recognition of the section *Setacea*, further resolution of *Batrachospermales* must await the addition of more taxa and characters.

In all shortest trees the brick-like rhizoidal filament cells (character 3 = 1) and large thallus apical cells (character 1 = 1) are derived character states within the *Batrachospermales s. str.* There is a single parallelism of the apical cell size character in *Lemanea fluviatilis*, but as noted under 'Characters' the scoring of character 1 in this taxon needs verification. The brick-like rhizoidal filament cells are a synapomorphy uniting *Batrachospermum latericum* and *B. diatyches*.

Indeterminate gonimoblast filaments (character 16 = 0) are homoplaseous in the consensus tree. As explained above, 'short' and 'long' indeterminate gonimoblast filaments could not be used as character states in this analysis. However, if shortly indeterminate gonimoblast filaments are plotted on the consensus tree, they occur only in the *B. turfosum-Setacea* clade. Further study should focus on the development and distribution of shortly determinate gonimoblast filaments, and the homology of long indeterminate gonimoblast filaments in *Thorea*, *Sirodotia* and *Nothocladus* (there is a reversal in this character between the *Thorea* and the latter taxa).

The use of distribution of spermatangia as a taxonomic character in section *Batrachospermum* has been analysed recently by Vis and Sheath (in press). Based on molecular and morphological data, Vis and Sheath (in press) reduce *B. spermato involucrum*, characterised by the presence of spermatangia on involucreal filaments as well as on vegetative fascicles, to a form of *B. gelatinosum*. In 'section *Setacea*', *B. androinvolucrum* produces spermatangia exclusively on involucreal filaments, while at least some populations of *B. atrum* have spermatangia on both involucreal filaments and vegetative fascicles. In Fig. 5, the presence of spermatangia on involucreal filaments (character 7 = 1) is a derived character but the tree is unresolved in relation to *B. androinvolucrum* and *B. atrum*. The circumscription of *B. atrum* is still unconvincing, and further characters are needed to define robust taxa in all but the *B. diatyches-B. latericum* group of the section *Setacea*.

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Appendix 1. Data matrix for phylogenetic analysis.

- = Not applicable

* = outgroups (as defined in Vis *et al.* 1998, fig. 3)

	0	5	10	15
* <i>Thorea violacea</i> 1	0 0 0 - 0	0 0 0 - 0	0 0 0 0 -	0 0 - - -
* <i>Thorea violacea</i> 2	0 0 0 - 0	0 1 0 - 0	0 0 0 0 -	0 0 - - -
<i>Batrachospermum macrosporum</i>	1 0 0 0 0	1 1 0 1 0	1 0 1 1 1	1 1 0 0 0
<i>Batrachospermum louisianae</i>	1 0 0 0 0	1 1 0 1 1	1 0 1 1 0	1 1 0 1 1
<i>Batrachospermum helminthosum</i>	1 0 0 0 0	1 1 0 1 0	0 0 1 1 1	1 1 0 1 0
<i>Batrachospermum turfosum</i> 1	1 0 0 0 0	1 0 0 1 0	0 0 1 1 0	- - - - -
<i>Batrachospermum turfosum</i> 2	1 0 0 0 0	1 0 0 1 0	0 0 1 1 0	1 0 0 1 0
<i>Nothocladus nodosus</i>	1 0 0 0 0	1 1 0 0 1	1 0 1 1 1	0 0 0 - -
<i>Batrachospermum boryanum</i>	1 0 0 0 0	1 1 0 0 0	1 0 1 1 0	1 1 1 0 0
<i>Sirodotia suecica</i>	1 0 0 0 0	1 1 0 1 0	0 1 1 1 1	0 0 0 - -
<i>Lemanea fluviatilis</i>	1 1 1 - 0	1 1 0 0 1	1 0 0 0 -	1 1 1 2 0
<i>Tuomeya americana</i>	1 0 1 0 1	1 1 0 1 1	1 1 1 1 1	1 1 0 1 0
<i>Batrachospermum gelatinosum</i>	1 0 0 0 0	1 1 0 0 0	1 0 1 1 0	1 1 1 0 0
<i>Batrachospermum atrum</i> 1	1 0 0 0 1	1 1 0 1 0	0 0 1 1 0	1 1 0 1 1
<i>Batrachospermum atrum</i> 2	1 0 0 0 1	1 1 1 1 0	0 0 1 1 0	1 1 0 1 1
<i>Batrachospermum atrum</i> 3	1 0 0 0 1	1 1 0 1 0	0 0 1 1 0	1 0 0 1 1
<i>Batrachospermum atrum</i> 4	1 0 0 0 1	1 1 1 1 0	0 0 1 1 0	1 0 0 1 1
<i>Batrachospermum puiggarianum</i>	1 0 0 0 1	1 1 0 1 0	0 0 1 1 0	1 1 0 1 1
<i>Batrachospermum androinvolucrum</i>	1 0 0 0 1	1 1 1 1 0	0 0 1 1 0	1 1 0 1 1
<i>Batrachospermum latericum</i>	1 1 0 1 1	1 1 0 1 0	0 0 1 1 0	1 1 0 1 1
<i>Batrachospermum diatyches</i>	1 1 0 1 1	0 1 0 1 0	0 0 1 1 0	1 1 0 0 1